PTERYGOMETOPINE TRILOBITES FROM THE ORDOVICIAN OF BALTOSCANDIA

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ABSTRACT. A revision of the Pterygometopinae from Baltoscandia has revealed that the subfamily is more diverse at the generic level than previously known. New genera are *Ingriops*, *Oelandiops*, *Upplandiops*, and *Keilapyge*. The earliest species of *Achatella* are included in the new subgenus *A.* (*Vironiaspis*). The new species *Oelandiops mirificus*, *Upplandiops calvus*, *Estoniops maennili*, and *E. fjaeckensis* are described. *Upplandiops calvus* differs from most other dalmanitaceans in having only ten thoracic segments.

THE Pterygometopinae, as defined by Ludvigsen and Chatterton (1982), has its centre of distribution in the Baltoscandian region and the western slope of the central and southern Ural Mountains. The subfamily began to spread to other regions, such as the British Isles and North America, comparatively late in the Middle Ordovician. The Early Ordovician records of *Pterygometopus* from Morocco (Destombes 1972) and Spain (Hammann 1972, 1974; Rabano 1989) have recently been revised (Henry *et al.* 1992) and shown to refer to early representatives of the family Dalmanitidae.

Previous knowledge of Baltoscandian pterygometopines is largely confined to Schmidt's (1881) monograph on species from northern Estonia and Ingria (the district in Russia between Estonia and Lake Ladoga; Text-fig. 1). The illustrations in the monograph are small-scale drawings with which even Schmidt himself was not quite satisfied. Männil (1958) established the genus *Estoniops*, provided adequate illustrations of the cephalon of *E. exilis* (Eichwald, 1858) and described a new species, *E. bekkeri*, but for the remainder of the East Baltic pterygometopines Schmidt's monograph remained the only available published source of information. The Swedish material of the subfamily has never been described except for the type species of *Pterygometopus*, redescribed by Whittington (1950), and the very rare species *P. sandbyensis* (Olin, 1906) and *P. schmidti* Warburg, 1925, each represented by a single, fragmentary cephalon. Wiman (1908) figured specimens believed by him to represent *Pterygometopus* (= *Estoniops*) *exilis*.

The intention of the present paper is a revision of the Baltoscandian pterygometopines at the genus level. In addition to previously undescribed type species of new genera, only a few new species are included. The available material contains some ten additional species which appear to be new, but the description of this material is a separate task, as is a phylogenetic analysis of the group.

The figured specimens of *Ingriops trigonocephalus* (Schmidt, 1881; Pl. 5, fig. 1) and *Estoniops panderi* (Schmidt, 1881) (Pl. 1, fig. 3) are from A. von Volborth's collection and were presented to the Swedish Museum of Natural History by F. Schmidt. They are identified by him on the labels, and quite obviously represent syntypes because Volborth's collection was one of F. Schmidt's main sources of material from Ingria. We do not attempt to designate lectotypes for these two species or for other species described by Schmidt (1881) which are considered in this paper. Designation of lectotypes should be done in the course of a substantial revision of the material available to F. Schmidt. Such a revision was outside the scope of the present paper.

TERMINOLOGY

The terminology used in this paper mainly follows that of Harrington *et al.* (*in* Moore 1959, pp. 117–126). We prefer 'dorsal furrow' and 'rachis' to 'axial furrow' and 'axis' because these were the

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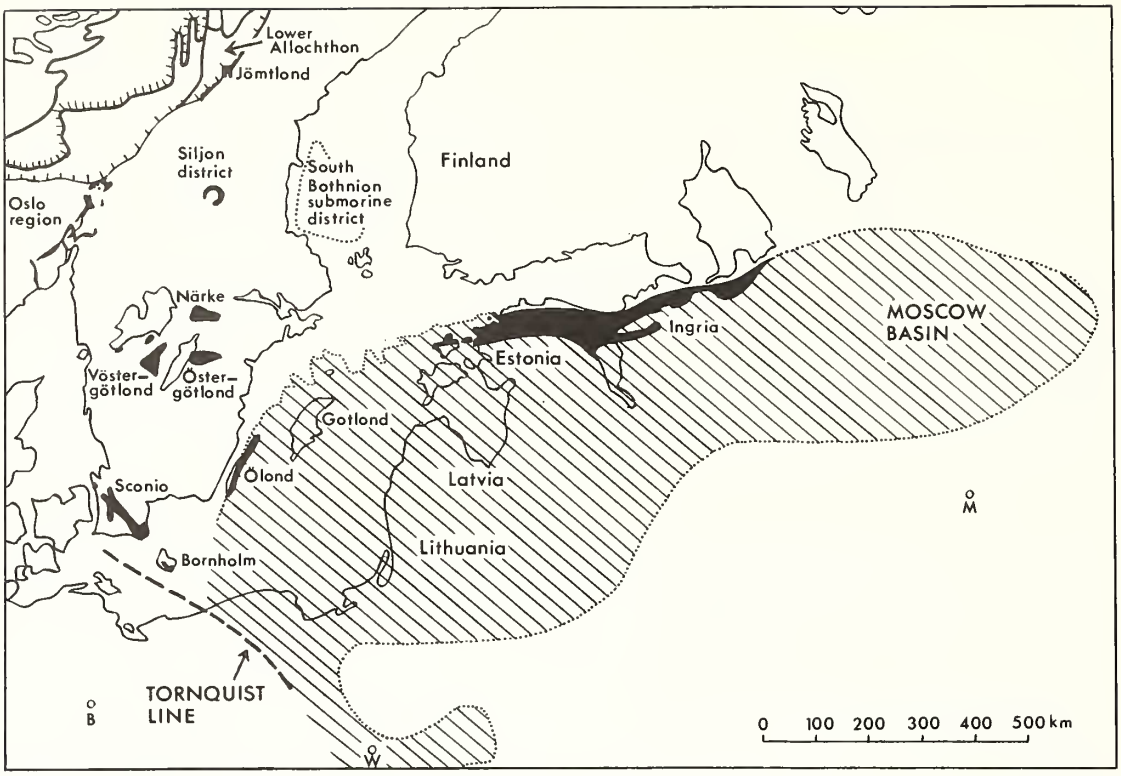


TEXT-FIG. 1. Districts of Ordovician outcrop in Baltoscandia (shaded black), and the extent of subsurface and submarine Ordovician on the Russian Platform (diagonal shading).

terms introduced by Dalman (1827) for these structures in the first systematic terminology of the trilobite exoskeleton (see also Jaanusson 1956). An additional reason in favour of 'rachis' is that it is difficult or impossible to use 'axis' in this sense in almost any western language other than English. Following Jaanusson (1956), lateral glabellar lobes (L) and furrows (S) are numbered from posterior to anterior

In many pterygometopines the frontal lobe of the glabella extends in lateral direction across the facial suture. The portion of the lobe lateral to the facial suture is here termed 'transsutural wing' of the lobe. In several pterygometopines which have transsutural wings, a ridge is developed at the cephalic margin. The ridge is most distinct anteriorly and fades gradually in posterolateral direction. A comparable ridge is known from other phacopaceans, in particular some Devonian phacopines (see, for example, Eldredge 1972). Ramsköld and Werdelin (1991, p. 39) termed the structure 'border ridge'. In this paper the term 'marginal cephalic ridge' is preferred because in pterygometopines the former term could be confused with the lateral cephalic border, which in many cases is ridge-like. The distinctness of the marginal ridge is in many species increased by a furrow behind the ridge, in this paper termed the 'admarginal cephalic furrow'.

Following Campbell's (1977, p. 71) procedure for dalmanitids, we try to avoid ambiguous counts of pleural ribs by counting the number of pleural furrows instead. We use the term rib only for comparative purposes.

SYSTEMATIC PALAEONTOLOGY

Repositories. Figured specimens are housed in the Swedish Museum of Natural History, Stockholm (prefixed RM Ar), the Institute of Geology, Estonian Academy of Sciences, Tallinn (ETAGI Tr), Museum of

Palaeontology, Uppsala University (PMU B and PMU D), and Type Collection, Geological Survey of Sweden (SGU).

Photography. Dorsal view of cephalon has been used as defined by Clarkson (1966) for phacopid trilobites. Other orientations follow Whittington and Evitt (1954). Photographs are of external surfaces of the exoskeleton, unless stated otherwise. All specimens were painted with matt black opaque and coated lightly with ammonium chloride prior to photography. All photographs are by the authors.

Family PTERYGOMETOPIDAE Reed, 1905

Diagnosis. See Ludvigsen and Chatterton (1982). Attention should be paid to the fact that the pygidium can have a semicircular outline, the number of rachial rings and pleural ribs can be as low as three, and that in the adults of some forms no interpleural furrows can be discerned.

Subfamily PTERYGOMETOPINAE Reed, 1905

Diagnosis. Frontal lobe laterally strongly expanded, reaching beyond the anteromedian extent of the visual surface of the eye. L1 and L2 of about equal length. Eye bases normally surrounded laterally by distinct subocular furrow. Pygidium with a semicircular to subparabolic outline.

Genera assigned. *Pterygometopus* Schmidt, 1881, *Ingriops* gen. nov., *Oelandiops* gen. nov., *Estoniops* Männil, 1958, *Upplandiops* gen. nov., *Keilapyge* gen. nov., *Achatella* (*Achatella*) Delo, 1935, *Achatella* (*Vironiaspis*) subgen. nov.

Discussion. Schmidt (1881, p. 76) distinguished three groups of species in *Pterygometopus*:

(1) *Phacops* (*Pterygometopus*) *sclerops* (Dalman) and *P.* (*P.*) *trigonocephala* Schmidt, each of which was defined in a wide sense and is now known to comprise several separate species. In this paper they are regarded as representing two genera, *Pterygometopus* and *Ingriops* gen. nov.

(2) *P.* (*P.*) *panderi* Schmidt, *P.* (*P.*) *exilis* (Eichwald) and *P.* (*P.*) *laevigata* Schmidt. For this group Männil (1958) established the genus *Estoniops*. Although *P.* (*P.*) *laevigatus* was included, he noted that this species belonged to a separate branch. We regard that branch as an independent, new genus, *Keilapyge*.

(3) *P.* (*P.*) *kuckersiana* Schmidt, *P. P. kegelensis* Schmidt and *P.* (*P.*) *nieszkowskii* Schmidt. Männil (1958) considered these species to belong to the genus *Achatella* Delo, 1935.

In addition, from the Middle Ordovician of Sweden there are two new species, each belonging to a new monotypic genus (*Oelandiops* gen. nov. and *Upplandiops* gen. nov.).

Phacops jamesii Portlock, 1843, from the Tramore Limestone of the Republic of Ireland, does not appear to fit into any of the above genera. Morris (1988) included the species in *Estoniops* but Salter's (1864, pl. 1, figs 39–41) figures show the frontal lobe of the glabella to be defined by a distinct preglabellar furrow which posteriorly joins the dorsal furrow as in *Pterygometopus*. A very long (exsag.) L3 appears to exclude it from the latter genus. We have not seen any material of this species.

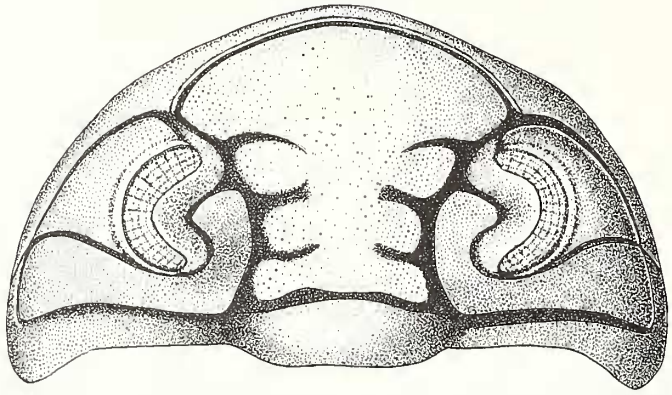
Pterygometopus huayinshanensis Lu, 1975, from the Neichiashan Series (stratigraphical unit within the series not recorded) of Szechuan in central China is known only from a single, fragmentary cephalon (Lu 1975, pl. 50, figs 6–10) in which details of several important morphological features remain unclear. The comparatively long (exsag.) eyes recall *Ingriops* gen. nov. but the genal angles are described as rounded and the development of the preglabellar furrow is not comparable with either *Ingriops* or *Pterygometopus*. A unique feature for a pterygometopine is the parallel-sided and posterolaterally inclined L3 which is only slightly longer (exsag.) than L2. The species may belong to a new genus.

All these forms belong to a fairly well-defined unit within the family Pterygometopidae, characterized by a laterally expanded frontal lobe of glabella, roughly equal length of the lateral

glabellar lobes L1 and L2 and (with one exception) by the presence of a distinct subocular furrow. The unit coincides with the subfamily Pterygometopinae as defined by Ludvigsen and Chatterton (1982), but it has a much greater taxonomic diversity at the generic level than known before. The known pterygometopines are all relatively small forms (maximum known cephalic length 16 mm).

Notes on pterygometopine morphology. The development of the anterior cephalic furrows and their topographic relationship to the anterior branch of the facial suture vary within the subfamily.

In *Pterygometopus* the frontal lobe of the glabella is defined by distinct dorsal and preglabellar furrows. The facial suture runs anteriorly and medially just in front of the preglabellar furrow (Text-fig. 2; faintly visible on the left side in Pl. 1, figs 1*a*, 2*a*; Whittington 1950, p. 539, fig. 3) so that the entire preglabellar furrow remains situated on the cranidium.



TEXT-FIG. 2. *Pterygometopus sclerops* (Dalman, 1827). Reconstruction of cephalon in dorsal view showing course of facial suture; based on lectotype RM Ar18074 (Pl. 1, fig. 2); lower Holen Limestone, Kunda Stage, probably lower *Asaphus raniceps* Zone; Husbyfjöl (Västanå), Östergötland, Sweden; ×4.

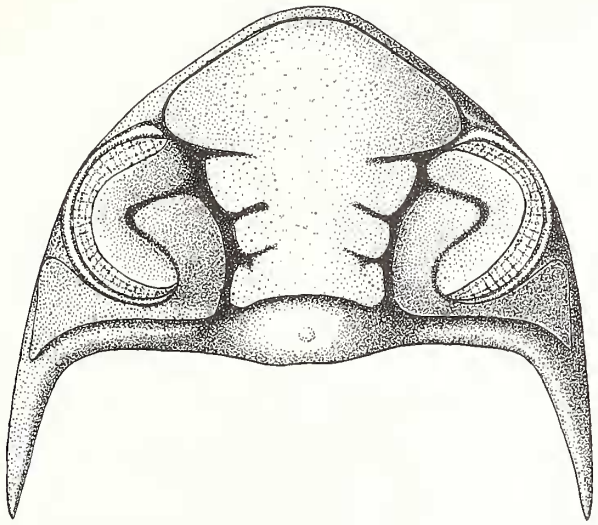
In *Ingriops* gen. nov. (Text-fig. 3) the arrangement of the anterior cephalic furrows has the same appearance as in *Pterygometopus*, but the facial suture runs in and not outside the preglabellar furrow. Thus the preglabellar furrow is situated at the anterior margin of the cranidium.

In most other pterygometopines the original preglabellar furrow is effaced laterally. There is then no distinct furrow to define the original lateral boundary of the frontal lobe of the glabella, although the location of the boundary is indicated in some species. In *Estoniops panderi*, for example, the anterior branch of the facial suture, in front of the dorsal furrow, is situated in a short, narrow and very shallow furrow (Pl. 1, fig. 3*c*). In *E. maennili* sp. nov. the original lateral extent of the frontal lobe is defined by a similar but still shorter furrow, but especially by the marked difference in sculpture on either side of the facial suture (Pl. 2, fig. 2). In several other species of *Estoniops*, such as *E. exilis* (Männil 1958, pl. 1, figs 1–6) and *E. fjaeckensis* sp. nov. (Pl. 4, fig. 2*a*), a definable boundary between the original frontal lobe and the transsutural wing cannot be distinguished in the relief of the dorsal exoskeletal surface. The transsutural wing tapers gradually posterolaterally until a faint ridge remains which can be followed between the cephalic admarginal and border furrows almost to the posterior branch of the facial suture (Pl. 4, figs 2*a*, 2*c*). In the current terminology transsutural wings are regarded as belonging to the frontal glabellar lobe, and in such species the lobe has an unusual extent. It should be emphasized that the inclusion of the transsutural wings in the frontal lobe does not imply that the former structures are homologous with any part of the frontal lobe as developed in forms in which the lobe is defined both anteriorly and laterally by a preglabellar furrow. The use of the extended definition of the frontal lobe is purely descriptive, necessitated by the lack of a discernible morphological boundary between the transsutural wings and the remainder of the frontal lobe.

In several species of *Estoniops*, such as *E. exilis* (Pl. 3, fig. 5; Männil 1958, pl. 1, figs 2–3, 5–6), *E. fjaeckensis* sp. nov. (Pl. 4, fig. 2) and *E. panderi* (Pl. 1, fig. 3), the anterior margin of the frontal lobe is formed by an admarginal cephalic furrow situated immediately behind the marginal cephalic ridge. In these forms the anterior branch of the facial suture runs, at least for a short distance medially, in the admarginal cephalic

furrow, suggesting that this portion (but not necessarily the remainder) of the furrow may be comparable to the preglabellar furrow as developed in *Pterygometopus* and *Ingriops*.

In *Keilapyge* gen. nov., *Upplandiops* gen. nov. and several species of *Estoniops* (*E. alifrons*, *E. maennili*, *E.* sp. nov. A) the marginal cephalic ridge and admarginal furrow are weak or absent medially, and the front of the glabella merges into the anterior cephalic border. In some forms, such as *Upplandiops calvus* (Pl. 3, figs 1*c*, 4*a*), even the boundary between the dorsal cephalic surface and the doublure is poorly defined.



TEXT-FIG. 3. *Ingriops trigonocephalus* (Schmidt, 1881). Reconstruction of cephalon in dorsal view, based on syntype RM Ar38514 (Pl. 5, fig. 1); Voka Beds?, Kunda Stage (*Didymograptus artus* Zone); Pavlovsk, Ingria, western Russia; × 4.

In *Achatella* the development of the preglabellar furrow varies from a condition comparable to *Pterygometopus* to a laterally completely effaced furrow and short (tr.) transsutural wings. The variability is discussed in the description of the genus.

Distribution. Removal of the Mediterranean forms from the pterygometopines (Henry *et al.* 1992) restricts the occurrence of the early representatives of the subfamily to the Baltoscandian region and the central and southern Ural Mountains (Antsygin 1970). They appear in the upper Arenig (*Didymograptus hirundo* Zone) and show the greatest diversity in the Middle Ordovician. First from the lower Caradoc on, representatives of the subfamily began to spread to other regions. The spread involved only a few genera: *Estoniops* occurs in northern Wales and north-western England, and *Achatella* in south-western Scotland, eastern and central USA (New York State, Illinois, Missouri, Ohio) and eastern Canada (Ontario and Quebec); for details see respective genera below and for North American occurrences see Ludvigsen and Chatterton 1982. Possible new genera are represented by *Phacops jamesii* Portlock, 1843 from south-eastern Ireland, and *Pterygometopus huayinshanensis* Lu, 1975, from Szechuan Province of China. The latest pterygometopine has been recorded from the Hirnantian of Scotland (Owen 1986).

Genus PTERYGOMETOPUS Schmidt, 1881

Type species. Calymene sclerops Dalman, 1827 (see discussion below); by subsequent designation of Bassler (1915, p. 1065).

Other species. Phacops (*Pterygometopus*) *sclerops* var. *angulata* Schmidt, 1881; *Pterygometopus bredensis* Weber, 1948. An additional species is here figured as *Pterygometopus* sp. nov. A (Pl. 1, fig. 1).

Diagnosis. Preglabellar furrow distinct, joining dorsal furrow laterally. Anterior branch of facial suture running just in front of preglabellar furrow; posterior branch situated in deep furrow. Eyes of moderate size, anteriorly reaching the dorsal furrow. Genal angles rounded. Vincular furrow distinct. Pygidial pleurae commonly faintly concave peripherally, with five to six pleural furrows.

Discussion. In Baltoscandia, *Pterygometopus* as defined in this paper has been identified routinely as a single species, *P. sclerops*. Schmidt (1881) pointed out the variability of the species but preferred to regard the variation as intraspecific. Only an especially distinctive form was distinguished as a separate variety, var. *angulatus*. Subsequent to Schmidt's (1881) monograph nobody is known to have taken a close look at the fairly comprehensive material, including many articulated specimens.

Examination of the material of *Pterygometopus* for this paper disclosed that it includes several well-defined, separate species. In the collections from the lower Holen Limestone of Östergötland (Sweden), the type horizon for *P. sclerops*, this species is not the commonest species of the genus. The type species is especially characterized by the presence of a wide, rounded anterior continuation of the palpebral lobe (Pl. 1, fig. 2), which considerably restricts the extent of the visual surface of the eye anteromedially. As a consequence, the anterior branch of the facial suture reaches the dorsal furrow far anteriorly, just behind the lateral end of the frontal lobe. In the other examined species of the genus the facial suture runs into the dorsal furrow at about the level of S3, and the visual surface of the eye extends farther anteromedially than in *P. sclerops*. This, for example, is the case with the species which is common in the *Asaphus expansus* Zone of Östergötland (*P.* sp. nov. A; Pl. 1, fig. 1). *P. sclerops* differs from the other, still undescribed species by a set of additional features, such as the relative height of the eyes, the configuration of the cephalic margin in anterior view and the surface sculpture. All examined species of *Pterygometopus* have a vincular furrow (Pl. 1, fig. 4; for *P. angulatus* see Schmidt 1881, pl. 1, fig. 12). In *P. sclerops* the vincular furrow is long and extends medially to the level of the lateral termination of the frontal lobe (Pl. 1, fig. 4).

The specimen figured by Dalman (1827, pl. 2, figs 1*a–c*) and refigured by Schmidt (1881, pl. 1, figs 3*a–c*, pl. 11, fig. 1), Whittington (1950, pl. 68, fig. 17, pl. 69, figs 1–3), Struve (*in* Moore 1959, fig. 388: 2*a–c*) and in this paper (Pl. 1, fig. 2) was termed holotype by Whittington (1950). However, when establishing the species, Dalman had several specimens at his disposal (Dalman 1827, p. 232) and thus the correct term of the type specimen is lectotype. The other specimens figured by Whittington (1950, pl. 68, figs 18–20) are not conspecific with the lectotype of *P. sclerops*.

Undoubted specimens of *P. sclerops* are known from the lower Holen Limestone of Östergötland, Närke and Västergötland. The available material from the Kunda Stage of Öland and the Siljan district is too fragmentary for a reliable identification at the species level. In the old collections from Husbyfjöl (= Västanå) and several other localities in Östergötland it is, because of similar lithology, difficult to determine whether the specimens come from the *Asaphus expansus* Zone or the lowermost *Asaphus raniceps* Zone. For this reason it is uncertain from which of these two units the lectotype of *P. sclerops* and conspecific specimens is derived. The same uncertainty holds true also

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EXPLANATION OF PLATE 1

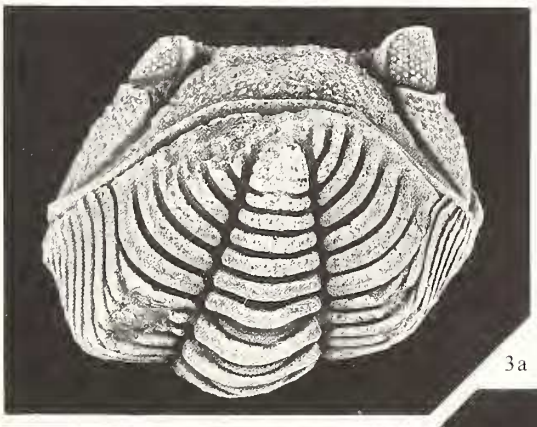
Fig. 1. *Pterygometopus* sp. nov. A; lower Kunda Stage, *Asaphus expansus* Zone; Kungs Norrby, Östergötland, Sweden; 1*a–b*, RM Ar18047; dorsal and anterior views of slightly abraded cephalon with part of thorax, × 4.

Figs 2, 4. *Pterygometopus sclerops* (Dalman, 1827); 2*a–b*, RM Ar18074, lectotype; lower Holen limestone, Kunda Stage, probably lower *Asaphus raniceps* Zone; Husbyfjöl (Västanå), Östergötland, Sweden; dorsal and anterior views of enrolled exoskeleton, × 3. 4, RM Ar55055; *Sphaeronites* Beds, Kunda Stage, lowermost *Asaphus raniceps* Zone; Råbäck quarry, Kinnekulle, Västergötland, Sweden; ventral view of part of cephalon showing vincular furrow, × 5.

Fig. 3. *Estoniops panderi* (Schmidt, 1881); Aseri Stage (lower *Didymograptus murchisoni* Zone); Pavlovsk, Ingria, western Russia; 3*a–c*, RM Ar38516; anterior, lateral and dorsal cephalic views of a syntype, enrolled exoskeleton, × 3.

1a

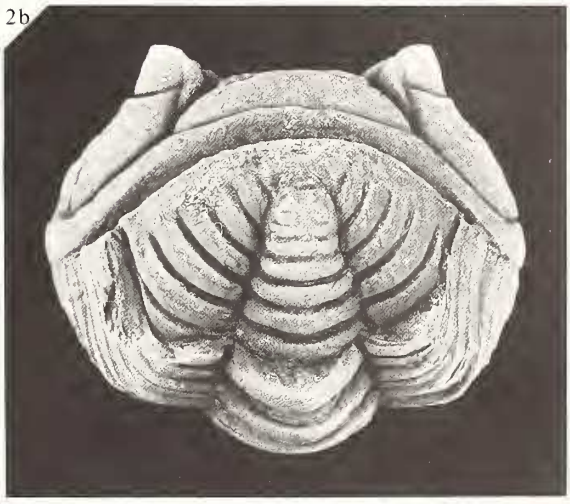
1b

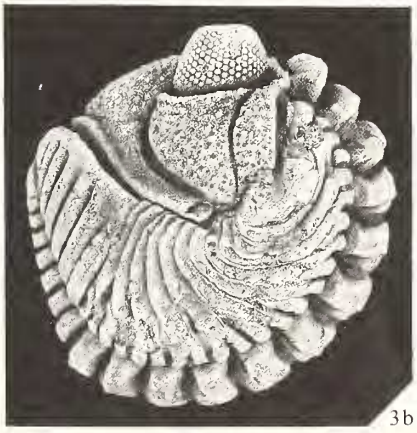


3a

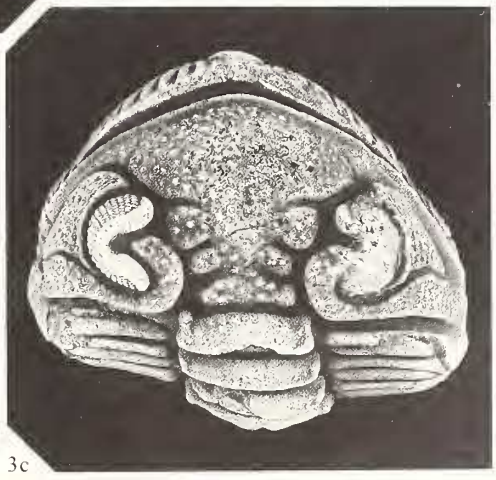
2a

2b





3b



3c

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JAANUSSON and RAMSKÖLD, *Pterygometopus*, *Estoniops*

with regard to specimens from Närke. However, on Kinnekulle in Västergötland *P. sclerops* occurs in the *Sphaeronites* Bed (RM Ar55055-Ar55056) which is within the lowermost *A. raniceps* Zone, and specimens of the genus collected by J. W. Dalman in 1827 at Ulunda brook on Billingen (RM Ar15507–Ar15510) are probably from beds of the same age. This indicates that the lectotype of *P. sclerops* may be from the lower part of the *Asaphus raniceps* Zone rather than from the *Asaphus expansus* Zone.

The Swedish material of *Pterygometopus* discussed above is from the lower and middle Kunda Stage. In Ingria, Lamansky (1905) recorded *P. sclerops* only from the middle and upper Volkhov Stage (corresponding to the *Megistaspis simon* and *M. limbata* Zones in the current Swedish biostratigraphic terminology). Ingrian specimens of *Pterygometopus* from the Volkhov Stage which were available for examination belong to *P. angulatus* Schmidt, 1881. This species differs clearly from *P. sclerops* and other forms from the Kunda Stage by the characteristically arched anterior cephalic margin and other features. On northernmost Öland *Pterygometopus* is not uncommon in the *Megistaspis limbata* Zone but the material is fragmentary. However, from Hälludden there is a cephalon (RM Ar55010; 0·80–0·85 m below the upper boundary of the *M. limbata* Zone) which shows the characteristic features of *P. angulatus*.

Occurrence. Middle and Upper Volkhov Stage (*Didymograptus hirundo* Zone) of Ingria and northern Estonia, Upper Volkhov Stage of Sweden (Öland). Lower and Middle Kunda Stage (*Didymograptus artus* Zone) of Ingria, northern Estonia, Sweden and the Oslo Region of Norway (Brögger 1882). Arenig calcareous sandstone of the Bredy region, eastern slope of southern Ural mountains (*P. bredensis*; Weber 1948; Antsygin 1970).

Genus INGRIOPS gen. nov.

Derivation of name. From Ingria, the latinized form of the old name for the district in Russia between Estonia and Lake Ladoga; Inkeri in Finnish, Ingermanland in Swedish. Gender masculine.

Type species. *Phacops* (*Pterygometopus*) *trigonocephala* Schmidt, 1881.

Other species. *Phacops* (*Pterygometopus*) *trigonocephala* var. *intermedia* Schmidt, 1881; *Phacops* (*Pterygometopus*) *trigonocephala* var. *estonica* Schmidt, 1881; *Phacops* (*Pterygometopus*) *trigonocephala* var. *genuina* Schmidt, 1881.

Diagnosis. Preglabellar furrow distinct, joining the dorsal furrow laterally. Anterior branch of facial suture running in the preglabellar furrow; posterior branch situated in a deep furrow. Eyes fairly long, 46 per cent of cephalic length in type species. Fixed cheeks with genal spines. Vincular furrow distinct. Pygidium with a subparabolic outline, pleural areas with ten or eleven pleural furrows.

Discussion. In Schmidt's concept, the array of forms which in this paper is included in *Ingriops* gen. nov. constituted a single variable species. He recognized that this 'species' is not taxonomically homogeneous by distinguishing various forms as varieties. Most, if not all, of these varieties represent separate species.

Lamansky (1905) recorded *Pterygometopus trigonocephalus* in the Ingrian sequence from the *Asaphus expansus* and *Asaphus raniceps* Zones, and suggested that both var. *estonicus* and var. *genuinus* from northern Estonia were younger, derived from the upper Kundan *Asaplus eichwaldi* (= *A. sulevi*) Zone. Schmidt (1881) reported *P. trigonocephalus* also from Husbyfjöl in Östergötland. In the Riksmuseum collections there is a fragmentary cephalon (RM Ar18016) of *Ingriops* from the lower Holen Limestone of this locality, on the accompanying label identified by F. Schmidt as '*P. trigonocephala*', but in Östergötland the genus appears to be very rare. A distinctive pygidium of *Ingriops* has been found in the topmost beds of the Kunda Stage (*Megistaspidella gigas* Zone) at Ljung in Östergötland (RM Ar18077).

At first sight the cephalon of *Ingriops* appears to be fairly similar to that of *Pterygometopus*. The conspicuous differences are the presence of genal spines and the larger eyes (in the eye of an adult *Ingriops trigonocephalus* there are 32 files of up to 13 lenses; Pl. 5, fig. 1*d*). A close examination reveals that in *Ingriops* the facial suture runs in and not in front of the preglabellar furrow (see also Schmidt 1881, pl. 1, fig. 15c). The vincular furrow in *I. trigonocephalus* was figured by Schmidt (1881, pl. 1, fig. 12).

The pygidium of *Ingriops* has a distinctive appearance. It is comparatively longer than in *Pterygometopus*, with a subparabolic outline and provided with far more numerous, flattened pleural ribs.

Occurrence. Kunda Stage (*Didymograptus artus* Zone) of Ingria, northern Estonia and the province of Östergötland in Sweden.

Genus OELANDIOPS gen. nov.

Derivation of name. From the Island of Öland, latinized Oelandia. Gender masculine.

Type species. Oelandiops mirificus gen. et sp. nov.

Other species. The genus is monotypic.

Diagnosis. Frontal glabellar lobe with short (tr.) transsutural wings. Marginal cephalic ridge and admarginal cephalic furrow well-defined. Anterior branch of facial suture reaches anteromedially admarginal furrow. Lateral glabellar lobes transverse. Posteromedian part of fixigena expanded abaxially into long (exsag.), wing-like structure overhanging dorsal furrow from S0 to S2. Genal angles rounded. Pygidium strongly convex with steeply sloping outer portion of the pleural areas and the postrachial area; pleural area concave along margin, with eight or nine deep pleural furrows, interpleural furrows distinct. Dense tuberculation on thorax and pygidium.

Discussion. Oelandiops gen. nov. is in many respects so different from the other pterygometopines that a detailed discussion of the distinguishing features is not necessary. It resembles *Estoniops*, especially *E. panderi*, in the extension of the frontal lobe laterally across the facial suture, but the transsutural wings of the lobe are short. The transverse orientation of L1 and L2 resembles that of *Upplandiops* gen. nov., but in other respects these two genera are very different. The pygidium is similar to that of *Pterygometopus* or *Estoniops panderi* but the postrachial area is steeply sloping.

Occurrence. As for the type species.

Oelandiops mirificus sp. nov.

Plate 2, fig. 1*a–g*

Derivation of name. Latin *mirificus*, amazing, astounding.

v.1960 Pterygometopinae n. gen. n. sp.; Jaanusson, pp. 225, 279.

Holotype. Complete enrolled exoskeleton (Pl. 2, fig. 1*a–g*), RM Ar47921, Binnerbäck, northern Öland. Segerstad Limestone, Zone of *Illaenus planifrons* (upper Aseri Stage; lower *Didymograptus murchisoni* Zone). No other specimens are known.

Diagnosis. As for genus.

Description. Glabella fairly flat between the palpebral lobes, cephalon steeply sloping anteriorly and laterally. Cephalic length (sag.) about 55 per cent of width. Lateral cephalic border highest along lateral margin of free

cheek, becoming gradually lower and less distinct anteromedially, fading posteriorly at level of posterior border furrow. Admarginal furrow apparently shallow medially (specimen broken), deepening considerably posterolaterally until merging with lateral border furrow somewhat in front of level of mid-length of eye.

Dorsal furrow deep, trench-like between eye and frontal lobe, widening along L3, tunnel-like between S2 and S0, there overhung by both the lateral extremities of L2 and L1 and the flat, wing-like medial projection of the fixed cheek. Frontal lobe of glabella extends laterally beyond the facial suture, but transsutural wing of lobe is fairly short and low, tapering in posterolateral direction until becoming gradually obsolete in front of level of mid-length of eye. Axes of lateral glabellar lobes almost transversely directed. S3 meets dorsal furrow slightly posterior to level of anterior margin of eye, fairly shallow, gently posteromedially curved. Maximum length of L3 (exsag.) about twice that of L2. Lateral edge of L3 fairly strongly convex outward, surface of posterior portion gently downwards sloping, posterolateral corner of lobe pointed (Pl. 2, fig. 1*g*). S2 deep, widening adaxially. L2 and L1 with flat dorsal surface which slopes slightly upward laterally (Pl. 2, fig. 1*g*), their rounded outer margins almost reaching flat, exsagittally and adaxially expanded, wing-like extension of fixed cheek. S1 bifurcates adaxially, with small, posteromedian branch defining inner margin of lateral node of L1 (Pl. 2, fig. 1*b*). Occipital ring laterally with an incipient, transversely directed furrow.

Palpebral lobes not quite reaching level of glabella in anterior view (Pl. 2, fig. 1*d*). Palpebral lobe extends anteriorly to dorsal furrow slightly in front of S1. Palpebral furrow deep. Eyes set wide apart; distance between inner margins of palpebral lobe anteriorly 1·6–1·7 times width (tr.) of occipital ring. Eye length (exsag.) about 35 per cent of cephalic length (sag.). Visual surface with 25 files of up to 10 lenses; best preserved eye has lens formula (from anterior) 456 788 989 9910 999 988 888 765 3. Subocular furrow deep, surrounded outwards by prominent rim which slightly overhangs adjacent field of free cheek (Pl. 2, fig. 1*d*). Anterior branch of facial suture running from eye exsagittally into dorsal furrow, ascends frontal lobe and continues in a wide arch, reaching admarginal furrow medially. Adaxial portion of posterior branch of facial suture situated in a furrow, lateral portion runs roughly parallel to posterior border furrow.

Only parts of doublure accessible for examination (Pl. 2, fig. 1*e*); no vincular furrow. Hypostome unknown.

Thorax of eleven segments. Inner part of pleurae horizontal, outer part almost vertically sloping (Pl. 2, fig. 1*e*). Rachial rings laterally with faint, transversely directed furrow (Pl. 2, fig. 1*b*, *e*). Pleural furrows deep, both anterior and posterior pleural bands relatively narrow and high.

Pygidium 1·7 times wider than long (excluding articulating half ring); width about 64 per cent and length about 67 per cent of respective cephalic dimensions. Width (estimated) of first rachial ring 37–39 per cent of pygidial width. Rachis fairly strongly convex (tr.), with seven rings well defined by apodeme-carrying inter-ring furrows, and a short posterior piece with a weakly discernible additional ring. Only inner pleural area visible in dorsal view (Pl. 2, fig. 1*e*), outer areas and postrachial area steeply to vertically sloping; border narrow but distinct, outwardly flexed. Pleural areas with eight pairs of deep pleural furrows; an additional pair of furrows on the postrachial area may be a ninth pair; furrows become obsolete at inner margin of border. Five distinct interpleural furrows curving strongly backwards distally to reach the succeeding pleural furrow (Pl. 2, fig. 1*c*). Between pleural ribs of eighth pair is a median unpaired, bilaterally concave, raised band.

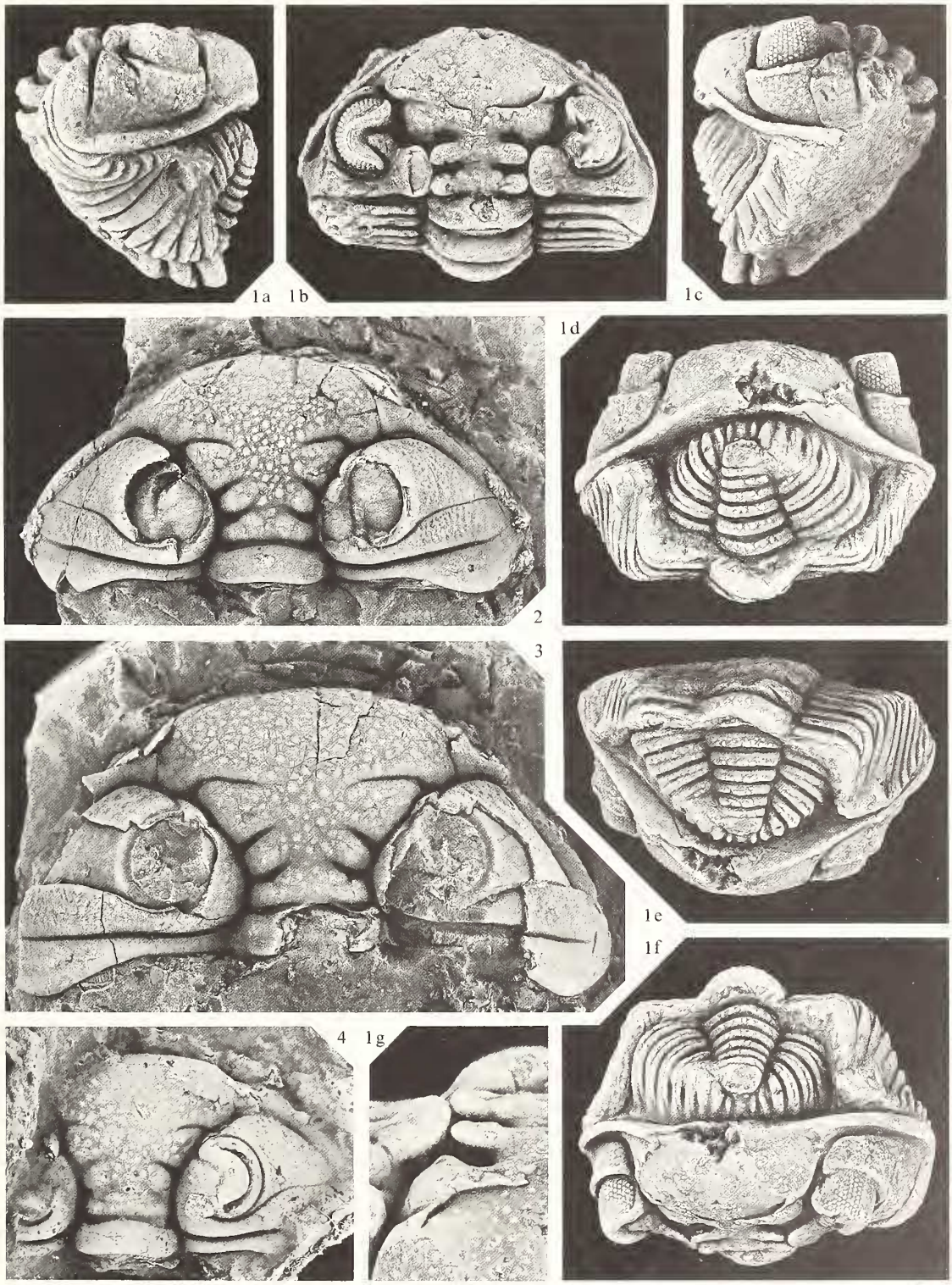
Sculpture which is not well preserved, consists of fairly coarse, apparently simple tubercles on all glabella, adaxial parts of fixed cheeks, free cheeks, thoracic and pygidial rachial rings and most of pleurae (except outermost parts). Cephalic marginal ridge and doublure with a fine granulation; such granulation may have extended to other parts of the exoskeleton but is not preserved. Pygidial border smooth.

Occurrence. As for the holotype.

EXPLANATION OF PLATE 2

Fig. 1. *Oelandiops mirificus* gen. et sp. nov.; Segerstad Limestone, Zone of *Illaenus planifrons* (upper Aseri Stage; lower *Didymograptus murchisoni* Zone); Binnerbäck, northern Öland, Sweden; 1*a–g*, RM Ar47921, holotype, enrolled exoskeleton; right lateral, dorsal cephalic, left lateral, anterior cephalic, dorsal pygidial, and posterior pygidial views, and detail of cephalon in oblique anterodorsal view, 1*a–f* × 3, 1*g* × 5·3.

Figs 2–4. *Estoniops maennili* sp. nov.; 2–3, Blidene Marl (lower *Dicranograptus clingani* Zone); western Latvia. 2, ETAGI Tr 2390, holotype; Adze boring (882·9 m); dorsal view, × 4. 3, ETAGI Tr 2368; Engure boring (932·9 m); dorsal view of large cephalon, × 3. 4, uppermost Skagen Limestone (lower *D. clingani* Zone); Kinnekulle, Mossen section, Västergötland, Sweden; RM Ar55054; dorsal view of latex cast of internal mould of cephalon, × 4.



JAANUSSON and RAMSKÖLD, *Oelandiops*, *Estoniops*

Genus ESTONIOPS Männil, 1958

Type species. Acaste exilis Eichwald, 1858 from the Kukruse Stage (*Nemagraptus gracilis* Zone) of northern Estonia; by original designation.

Discussion. Antsygin (1970, p. 17) designated the cephalon ETAGI Tr. 1902 figured by Männil (1958, pl. 1, figs 1–3) as the lectotype of *E. exilis*. The designation is not valid because this cephalon was not available to Eichwald (1858) when he described the species. The designation of a type specimen must await a revision of Eichwald's material.

Other species. Phacops (*Phacops*) *alifrons* M'Coy, 1851; *Phacops* (*Pterygometopus*) *panderi* Schmidt, 1881; *Phacops sandbyensis* Olin, 1906; *Estoniops bekkeri* Männil, 1958; *Estoniops oculeus* Antsygin, 1970; *Estoniops fjaeckensis* sp. nov.; *Estoniops maennili* sp. nov.

The examined material includes several additional species of *Estoniops*, such as the specimens figured as *Phacops exilis* by Wiman (1908, pl. 7, figs 1–5) from the Dalby Limestone of the erratics in Uppland derived from the South Bothnian submarine Cambro-Ordovician sequence (called *E.* sp. nov. B below), *E.* sp. nov. A (Pl. 3, figs 2, 7) from the Lasnamägi Stage of the File Haidar boring of Gotland, and a species represented by a fragmentary cranidium (PMU ÖI. 1010) from the Folkeslunda Limestone of the same stage of northern Öland (referred to as *Estoniops* sp. or *E.* aff. *panderi* by Jaanusson 1960, pp. 226, 278). A somewhat deformed cephalon (Paleontologisk Museum Oslo, no. 69526) from the lower part of the Nakkholmen Mudstone of Asker in the Oslo region (western side of the first tunnel at the Billingstad station) obviously belongs to an additional new species of *Estoniops*.

Diagnosis. Frontal lobe of glabella laterally not defined by a continuous furrow; it either extends across the facial suture into transsutural wings or is defined along the facial suture by a distinct change in sculpture. L3 triangular, much longer (exsag.) than L2; axis of L2 distinctly posterolaterally inclined. Eyes of medium size to fairly large, anterior end of palpebral lobe normally reaching dorsal furrow. Genal angles rounded. Pygidium with roughly semicircular outline, pleural area commonly evenly convex but may be faintly concave peripherally, with five to eight pleural furrows.

Discussion. Definition of the generic characters of *Estoniops* is rendered difficult by the existence of several species which show somewhat unusual features but which are poorly known either because of a poor state of preservation or inadequate illustrations.

The cephalon of the type species was adequately figured by Männil (1958, pl. 1, figs 1–6). Juvenile specimens (Pl. 3, fig. 5*a–c*) have a conspicuously shorter L3 than in adult cephala (Männil 1958, pl. 1, fig. 1) and approach in this respect the condition in *Pterygometopus*. The pygidium (Pl. 3, figs 8–9; Pl. 4, fig. 7) has four well-defined rachial rings and a posterior portion with one or two faint rings; pleural areas are evenly convex and provided with five pairs of faintly furrowed ribs of which the most posterior pair is indistinct.

Öpik (1937, p. 73) pointed out that in *E. exilis* the palpebral furrow unites directly with the dorsal furrow, that is, the anterior end of the palpebral lobe extends to the dorsal furrow. In *Estoniops* this is normally the case. The specimens from the upper Middle Ordovician Chergyn Stage of the Nizhnie Sergi district, western slope of the central Ural mountains, which Antsygin (1970, pl. 4, figs 7–16) identified as *E. exilis*, differ by having the anterior end of the distinctly smaller eyes situated some distance from the dorsal furrow (Antsygin 1970, pl. 4, figs 7–8). Other differences include a more strongly posterolaterally inclined L2, a shorter (sag.) occipital ring and, especially, the continuation of the pleural furrows to the pygidial margin. In *Estoniops* there is normally a distinct, narrow border on the pygidium. The absence of a border in combination with the other differences casts some doubt on the generic affinity of the Uralian species, but the material is not well preserved and the quality of the photographs not sufficient for safe conclusions. *Estoniops*? *angulatus* Antsygin, 1970 (pl. 5, figs 17–18) from the same stage of the central Ural mountains seems to be a related species of the same doubtful generic affinity.

The earliest species of *Estoniops*, *E. panderi* (Schmidt, 1881) from the Aseri Stage (lower *Didymograptus murchisoni* Zone) of Ingria and Estonia (Pl. 1, fig. 3*a–c*), shows some *Pterygometopus*-like features. It has a relatively short (exsag.) L3, the posterior branch of the facial suture runs in a furrow, the cephalic dorsal furrows are very deep, and the pygidium is *Pterygometopus*-like with peripherally distinctly concave pleural areas (Pl. 1, fig. 3*a*). In the visual surface there are 21 files of up to 9 lenses.

The specimens from the upper Middle Ordovician Chergyn Stage of the Nizhnie Sergi district, western slope of the central Ural mountains, that Antsygin (1970, pl. 5, figs 1–5) identified as *E. panderi* (a much earlier species) cannot possibly be conspecific with the latter. They have no admarginal cephalic furrow visible in dorsal view, a long and triangular L3, a shallow S3, evenly convex pygidial pleural areas, and a smaller number of both rachial rings and pleural ribs in the pygidium.

An advanced type of *Estoniops* appeared early, represented in the material by *E.* sp. nov. A. The somewhat fragmentary cephalon (Pl. 3, fig. 2), from the Lasnamägi Stage (upper *Didymograptus murchisoni* Zone) of the subsurface of Gotland, appears to lack a marginal cephalic ridge and an admarginal cephalic furrow, L3 is relatively long, and the associated pygidium (Pl. 3, fig. 7) has only four pleural furrows (plus a hint of a fifth) and virtually effaced interpleural furrows.

In *Estoniops* as defined in this paper the development of the marginal cephalic ridge and the admarginal cephalic furrow varies. The ridge is distinct in *E. exilis* (Pl. 3, fig. 5*c*; Männil 1958, pl. 1, figs 2, 5), *E. fjaeckensis* sp. nov. (Pl. 4, fig. 2*b*), and in *E. panderi* (Pl. 1, fig. 3), somewhat less distinct in the cephalon figured as *E. exilis* by Wiman (1908, pl. 7, fig. 1; *E.* sp. nov. B in this paper). In several species, such as *E. alifrons* (Whittington 1962, p. 17), *E. maennili* sp. nov. and probably also in *E.* sp. nov. A (Pl. 3, fig. 2), the furrow is obsolete, and no distinct marginal cephalic ridge is developed. Due to the poor quality of illustrations or insufficient state of preservation the development of the marginal cephalic ridge and the admarginal furrow is unclear in most species of *Estoniops* described by Antsygin (1970).

Occurrence. The known vertical range of *Estoniops* is from equivalents of the lower *Didymograptus murchisoni* Zone (Aseri Stage) to the lower *Dicranograptus clingani* Zone (Blidene Marl, Skagen Limestone, Upper Llongvillian). Baltoscandia (Ingria, Estonia, Latvia, Sweden, Oslo region in Norway); Wales, Bala district (lower Bala series, uppermost Gelli-grîn Group; *E. alifrons* in Whittington 1962); northern England, Cross Fell Inlier (Upper Longvillian; *E. alifrons* in Dean 1962); western slope of the central Ural mountains (Chergyn Stage: *E. panderi* in Antsygin 1970; Tupyl Stage: *E. oculeus* Antsygin, 1970).

Estoniops fjaeckensis sp. nov.

Plate 4, figs 2, 6

Holotype. A cephalon (Pl. 4, fig. 2*a–c*), RM Ar53596, Fjäcka section, Siljan district, Skagen Limestone, 1·6 m from the lower boundary.

Other material. Four pygidia from the Fjäcka section (RM) which presumably belong to *E. fjaeckensis*, but are all juvenile (Pl. 4, fig. 6). No distinct differences from those of *E. exilis* can be observed.

Diagnosis. Admarginal cephalic furrow and transsutural wings of relatively weakly convex frontal lobe of glabella extend posterolaterally almost to the posterior branch of the facial suture. Eyes fairly long, about 47 per cent of the cephalic length; comparatively low. Occipital ring comprises about 19–20 per cent of cephalic length. Outer portion of posterior branch of facial suture converges laterally with posterior border furrow. Tubercles composite, with superimposed granulation.

Description. The species is similar to the much older *E. exilis*; emphasis is therefore put on distinguishing characters.

Cephalon is represented only by the holotype. The configuration of the cephalon in front of the eyes is similar to that of *E. exilis* except that the frontal lobe of the glabella is less convex. Transsutural wing of the frontal

lobe long, tapering posterolaterally into a weak ridge which reaches the posterior branch of the facial suture (Pl. 4, fig. 2*c*). The extent of the distinct admarginal furrow coincides with that of the frontal lobe. Eyes longer (about 47 per cent of cephalic length) than in *E. exilis* (fairly consistently 44 per cent of cephalic length) and comparatively lower. Visual surface of 19 files of up to 7 or 8 lenses, lens formula (from anterior) approximately 456 778 777 777 666 554 3 (some areas damaged). Anterior end of palpebral lobe extends to dorsal furrow somewhat in front of level of S3 (Pl. 4, fig. 2*a*), as in juvenile *E. exilis* (Pl. 3, fig. 5*a*) but farther anteriorly than in adults of that species (Männil 1958, pl. 1, figs 1, 4). This holds true also for the level at which the facial suture reaches the dorsal furrow. Occipital ring fairly long (19–20 per cent of cephalic length) compared to *E. exilis* (16 per cent of cephalic length) and rather wide (tr.). The posterior branch of the facial suture turns first almost straight anterolaterally, then curves fairly abruptly in posterolateral direction and continues straight to the lateral border furrow, converging with the course of the posterior border furrow (Pl. 4, fig. 2*c*). In *E. exilis* the outer portion of the facial suture runs almost straight in lateral direction parallel to the posterior border furrow (Pl. 3, fig. 5*b*; Männil 1958, pl. 1, figs 1, 3, 6). In both *E. fjaeckensis* and *E. exilis* the glabella carries fairly coarse tubercles of various sizes, but in *E. exilis* the tubercles are simple whereas in *E. fjaeckensis* they are composite, with a fine granulation encroaching onto or covering the tubercles.

Occurrence. Lower Skagen Limestone (probably equivalent to the topmost *Diplograptus multidens* Zone). Sweden, Siljan district, Fjäcka section.

Estoniops maennili sp. nov.

Plate 2, figs 2–4; Plate 4, fig. 4

v.1968 *Estoniops* cf. *alifrons* (M'Coy); Männil *et al.*, p. 89.

Derivation of name. After Dr Ralf Männil who collected most of the Latvian material and recognized the affinities of the species.

Holotype. Cephalon (Pl. 2, fig. 2) ETAGI Tr. 2390, from the Blidene Marl, Adze boring (882·9 m), western Latvia.

Other material. Four cephala and two pygidia from borings in western Latvia (ETAGI); two cephala, three cranidia, and two pygidia from Västergötland (RM) (see 'occurrence' below).

Diagnosis. Cephalon in front of eyes moderately convex, without a distinct marginal cephalic ridge. Frontal glabellar lobe laterally defined by distinct change in sculpture at facial suture. Eyes comparatively low, about 39–40 per cent of cephalic length; palpebral lobe narrow anteriorly. Occipital ring with a low median tubercle. Pygidial pleural areas with seven to eight pleural furrows,

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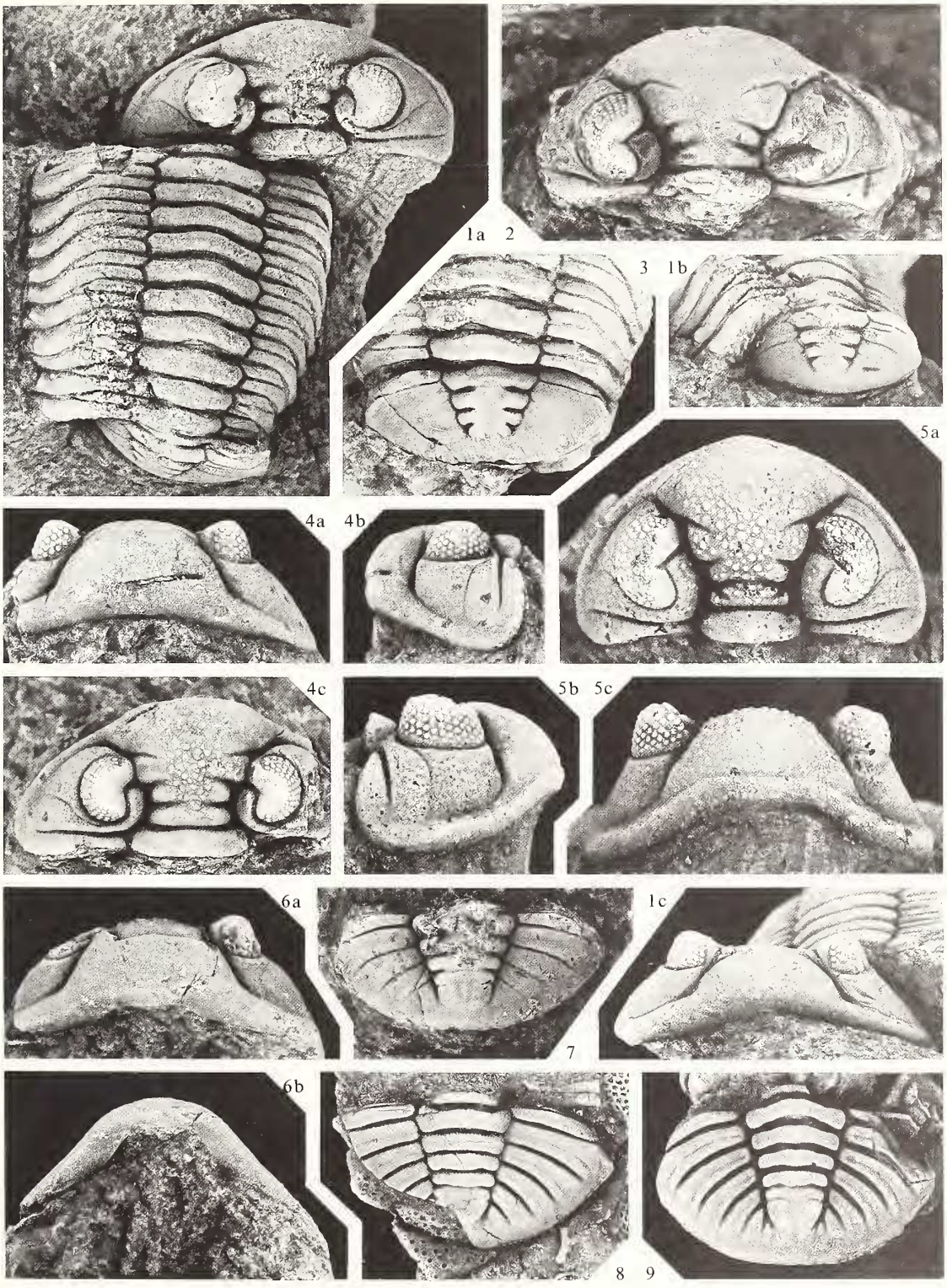
EXPLANATION OF PLATE 3

Figs 1, 3–4, 6. *Upplandiops calvus* gen. et sp. nov.; Furudal Limestone, Uhaku Stage, *Hustedograptus teretiusculus* Zone); Uppland province, Sweden; 1*a–c*, RM Ar55040, holotype; erratic boulder, Estuna; complete, slightly disarticulated exoskeleton, dorsal and anterior cephalic, and exterior pygidial views, × 6. 3, RM Ar55042; erratic boulder, Bergsbrunna 1; dorsal view of posterior part of articulated exoskeleton, central part of pygidial rachis apparently not abraded, × 6. 4*a–c*, RM Ar55041; erratic boulder, Bergsbrunna 1; anterior, lateral, and dorsal views of cephalon, × 6. 6*a–b*, UM B580; erratic boulder no. 4; Börstil parish, Höganäs, Torrön; anterior, and ventral views of incomplete cephalon, × 6.

Figs 2, 7. *Estoniops* sp. nov. A; Lasnamägi Stage (Upper *Didymograptus murchisoni* Zone); File Haidar boring (level 337·35–337·49 m), Gotland, Sweden; 2, SGU Type 8429*a*; dorsal view of cephalon, × 6. 7, SGU Type 8429*b*; dorsal view of pygidium, × 4.

Figs 5, 8–9. *Estoniops exilis* (Eichwald, 1858); Viivikonna Formation, Kiviõli Member, Kukruse Stage (*Nemagraptus gracilis* Zone); northeastern Estonia. 5*a–c*, RM Ar51262; Kukruse; dorsal, lateral, and anterior views of juvenile cephalon, × 10. 8, RM Ar55066; Kohtla-Järve; dorsal view of incomplete pygidium, × 5. 9, RM Ar55065; Küttejõu; exterior view of pygidium, × 4.



JAANUSSON and RAMSKÖLD, *Upplandiops*, *Estoniops*

eighth furrow very weak. Surface sculpture of cranidium includes fairly closely spaced tubercles with superimposed granules.

Description. *E. maennili* sp. nov. is in many respects similar to *E. alifrons*, described in detail by Whittington (1962), and therefore emphasis is put on the features which differ between these two species or which were not mentioned in the description of *E. alifrons*.

E. maennili attains a size which is large for *Estoniops*; a cranidium from Västergötland reaches a length (sag.) of 16 mm, and the largest known cephalon from Latvia (Pl. 2, fig. 3) is 14 mm long. In material from both Latvia and Västergötland, frontal lobe of glabella is moderately and fairly evenly convex. No admarginal cephalic furrow observed, nor any distinct marginal cephalic ridge. S3 curves posterolaterally just before reaching the dorsal furrow. Posterolateral margin of frontal lobe between S3 and facial suture slightly but fairly distinctly convex, especially in large specimens. Posterolateral boundary of frontal lobe also indicated by an incision or short furrow at facial suture, apparently a remnant of the preglabellar furrow. Remainder of lateral boundary of frontal lobe defined by clear difference in sculpture on either side of facial suture. Frontal lobe between anteriorly directed branches of the facial suture with closely spaced tubercles; lateral to the suture the sculpture consists solely of fine granulation. Lateral cephalic border rounded, anteromedian portion expanded so that when reaching frontal glabellar lobe the border forms a lateral continuation of that lobe with regard to width (exsag.) and convexity. Expanded portion of cephalic border resembles transsutural wings but there is no clear boundary between that portion and remainder of border. L2 more strongly posterolaterally inclined than in other species of *Estoniops*, excepting *E. alifrons*. Occipital ring with a low median tubercle. Posterior branch of facial suture runs in a furrow lateral to the eyes, deepest medially, gradually shallowing laterally. All these morphological details can be observed also in *E. alifrons* (Whittington 1962, pl. 3, fig. 6).

Distance (exsag.) between posterior margin of eye and posterior cephalic margin about 38–39 per cent of length of eye. The eyes appear to be fairly low, although because of slight deformation caused by compaction, their precise height is difficult to determine. Visual surface carries 22 files of up to 6 or possibly 7 lenses. Anterior extension of the palpebral lobe distinct in anterior view but very narrow. Subocular furrow well defined.

Sculpture of glabella consists of closely spaced tubercles of somewhat varying size, between and on which is a fine granulation extending also to the borders. Genal field with irregular pits.

Anterior six inter-ring furrows of pygidial rachis deep, with apodemes. Posterior portion carries fairly distinct seventh inter-ring furrow and indistinct eighth. Inner portion of pygidial pleural areas fairly flat, outer portion comparatively steeply sloping, with a weak indication of a peripheral concavity (Pl. 4, fig. 4*b*). Seven deep pleural furrows define six flat ribs; eighth pleural furrow faintly discernible. Interpleural furrows faint, observed on specimens both from Latvia and Västergötland; not recognizable on internal moulds. Surface of whole pygidium with fine granulation, densest along the outer margin (Pl. 4, fig. 4*b*).

Discussion. Specimens, preserved as internal and external moulds, from mudstone intercalation of the uppermost Skagen Limestone of Kinnekulle (Pl. 2, fig. 4) and northern Mösseberg in

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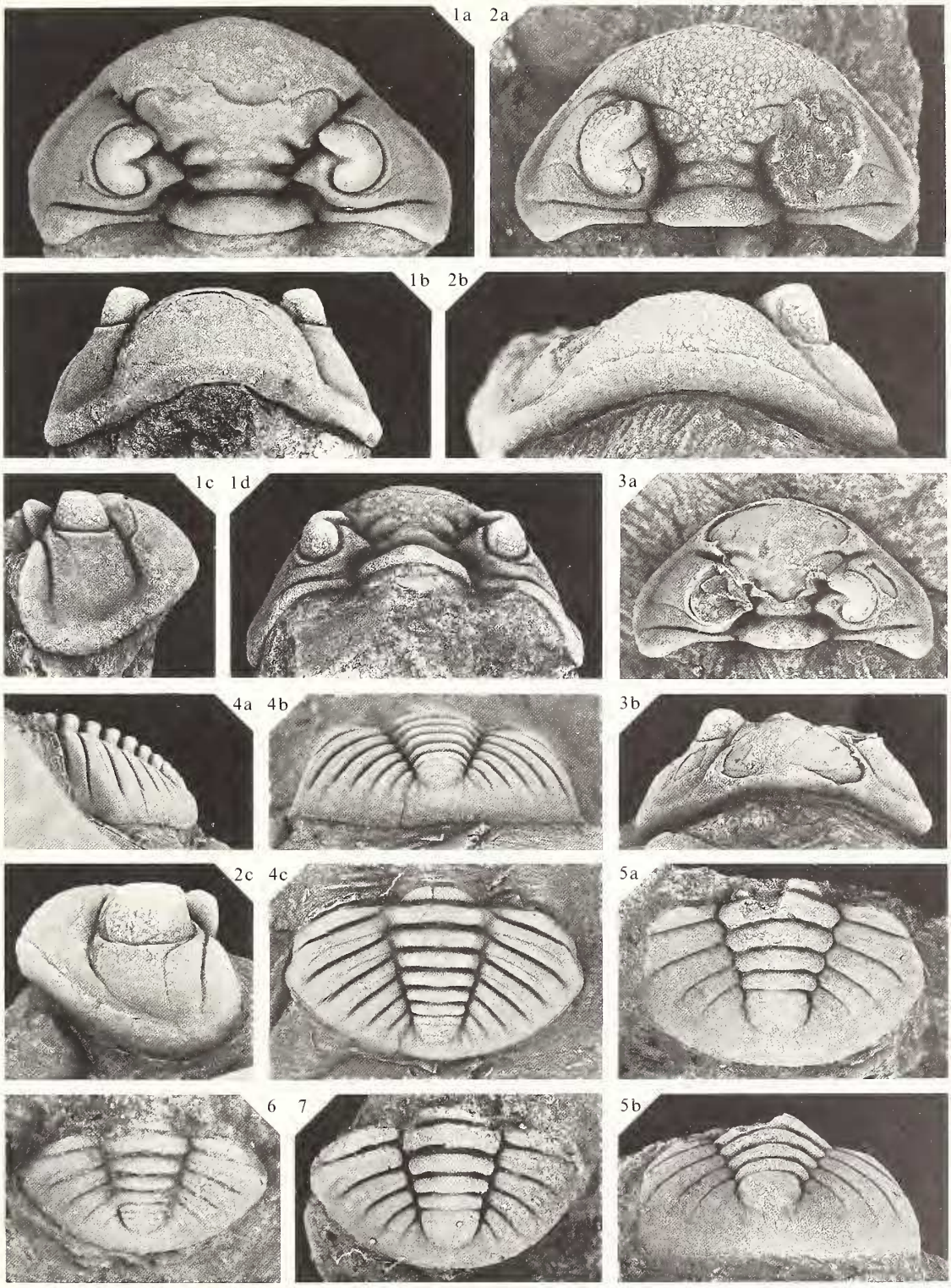
EXPLANATION OF PLATE 4

Figs 1, 3, 5. *Keilapyge laevigata* (Schmidt, 1881); Jõhvi and Keila Stages (uppermost *Diplograptus multidens* to lowermost *Dicranograptus clingani* Zones); northern Estonia. 1*a–d*, ETAGI Tr 1488; Ristna Beds of the Keila Stage; Pääsküla; dorsal, anterior, lateral, and oblique posterior views of cephalon; 1*a*, × 5; 1*b–d*, × 4. 3*a–b*, RM Ar54513; horizon and locality as fig. 1; dorsal, and anterior views of partly exfoliated cephalon, × 5. 5*a–b*, RM Ar55039; Jõhvi Stage; Aluvere; exterior, and posterior views of pygidium, × 4.

Figs 2, 6. *Estoniops fjaeckensis* sp. nov.; Fjäcka section, Siljan district, Sweden. 2*a–c*, RM Ar53596; Skagen Limestone, 1·6 m above lower boundary; dorsal, anterior, and lateral views of holotype cephalon, × 5. 6, RM Ar53597; uppermost Dalby Limestone, bed 12 of the bentonite sequence; dorsal view of small pygidium, × 13.

Fig. 4. *Estoniops maennili* sp. nov.; Blidene Marl (lower *Dicranograptus clingani* Zone); Blidene boring (892–893 m), western Latvia. 4*a–c*, ETAGI Tr 3610; lateral, posterior, and exterior views of pygidium, × 6.

Fig. 7. *Estoniops exilis* (Eichwald, 1858); Viivikonna Formation, Kiviõli Member, Kukruse Stage (*Nemagraptus gracilis* Zone); Kukruse, northeast Estonia; RM Ar50492; exterior view of small pygidium, × 9.



JAANUSSON and RAMSKÖLD, *Keilapyge*, *Estoniops*

Västergötland agree in all observable details with the specimens from the Blidene Marl of western Latvia.

As recognized by Ralf Männil, *E. maennili* is very similar to the roughly contemporary *E. alifrons*. Both species are large not only for the genus but for the whole subfamily, the sculpture is practically identical, and both have a low occipital tubercle. Neither species has a marginal cephalic ridge or an admarginal cephalic furrow. In both species the posterior branch of the facial suture is associated with a furrow, and both have a fairly steeply posterolaterally inclined L2. These two species belong to a separate group within the genus, distinguished especially by the morphology of the frontal glabellar lobe and the rounded lateral cephalic border.

E. alifrons has a well-defined, broad anterior extension of the palpebral lobe (Whittington 1962, p. 17, pl. 3, figs 6, 8). In *E. maennili* this structure is very narrow, and the visual surface of the eye extends farther medially. *E. alifrons* has higher eyes. In *E. maennili* there are 22 lens files of up to 6 or possibly 7 lenses, while in *E. alifrons* there are up to 11 or more lenses per file (exact number of files unknown but, as judged from illustrations, apparently close to that in *E. maennili*). Specimens of *E. alifrons* from both the Bala district and the Cross Fell Inlier (UK) are deformed to a varying degree, and this makes a detailed comparison with the only slightly compressed specimens from the Blidene Marl and uppermost Skagen Limestone difficult. The impression from the figured specimens identified as *E. alifrons* is that the species has a distinctly more steeply sloping frontal lobe and cheeks than in *E. maennili*.

E. sandbyensis Olin (1906, pl. 1, fig. 7) from the Sularp Shale (*Diplograptus multidens* Zone) of the Fogelsång district in Scania is represented by a single, somewhat compressed, fragmentary cephalon (Geological Institute, Lund Univ. LO 1901T), preserved mainly as internal mould. Without access to further material it is difficult to define the species. The genal angles are not preserved, and there is no evidence for the genal spines indicated by Olin (1906, pl. 1, fig. 7) on his drawing. A point of difference from *E. maennili* is the sculpture which in *E. sandbyensis* appears to consist of much more sparsely scattered large tubercles than in the former species.

The roughly contemporary *E. fjaeckensis* sp. nov. from the Skagen Limestone of the Siljan district has both a distinct marginal cephalic ridge and an admarginal cephalic furrow and is also otherwise clearly different.

Occurrence. Blidene Marl (lower *Dicranograptus clingani* Zone) of western Latvia: Adze boring (882·9 m), Blidene boring (892–893 m, 893·2 m), Engure boring (932·9 m, 934·0 m), Remte boring (1036·6–1038 m). Uppermost Skagen Limestone (lower *D. clingani* Zone), Västergötland, Sweden: Kinnekulle, Mossen section; Mösseberg, Jonstorp section.

Genus UPPLANDIOPS gen. nov.

Derivation of name. After Uppland (latinized Upplandia), the province in central Sweden where the type species is fairly common in erratic boulders of the Furudal Limestone, derived from the South Bothnian submarine Cambro-Ordovician sequence. Gender masculine.

Type species. Upplandiops calvus gen. et sp. nov.

Other species. The genus is monotypic.

Diagnosis. Anterior cephalic margin broadly rounded in section, without marginal ridge. Axes of glabellar lobes transversely directed, L3 only slightly longer (exsag.) at dorsal furrow than L1 and L2. Eyes fairly large. Genal angles rounded. No vincular furrow. Ten thoracic segments. Pygidium small relative to size of cephalon, posterior margin broadly rounded. Three pairs of laterally well defined but medially obsolete rachial rings and a posterior portion; pygidial pleural areas weakly convex, with three pairs of short (tr.), shallow pleural furrows.

Discussion. The configuration of the lateral glabellar lobes of *Upplandiops* resembles that of *Oelandiops* gen. nov., but otherwise these two genera are very different. In *O. mirificus* the dorsal

furrow is wide and deep opposite L3, whereas in *U. calvus* the corresponding sector is constricted and the dorsal furrow runs in a tunnel below a bridge formed by L3 and the anterior part of the palpebral lobe. In anterior view the cephalon of *Upplandiops* is somewhat similar to that of some species of *Estoniops* that lack a marginal cephalic ridge, but in a strictly dorsal view the frontal lobe of the glabella in *Upplandiops* does not give the impression of being extended across the facial suture into lateral wings, because at the facial suture the boundary between the frontal lobe and the lateral cephalic border is marked by a change in convexity.

The genus, or at least the type species of the genus, is especially remarkable in having only ten thoracic segments. In the suborder Phacopina the normal number of thoracic segments is eleven, and Struve (*in* Moore 1959) stated this number of segments to be diagnostic for the whole suborder. However, a few exceptions have been recorded. Maksimova (1957) reported ten thoracic segments in a species of *Isalaux*, known only from a single specimen. Another species of *Isalaux* has eleven segments (Frederickson and Pollack 1952). Ten segments were reported also in the single complete exoskeleton of a species of *Isalaux* (*Isalauxina*) by Maksimova (1962), a number confirmed by material figured by Semenova (1984). *Isalaux* is a pterygometopid genus that cannot at present be assigned to a subfamily (Ludvigsen and Chatterton 1982). A further pterygometopid with ten thoracic segments is the type species of the eomonorachine genus *Liocnemis*, *L. recurvus* (Linnarsson, 1869; see Kielan 1960). Since the above genera are not closely related, the reduction in the number of thoracic segments to ten must have taken place independently in several different lineages.

Upplandiops has, relatively, the smallest pygidium among pterygometopines. In *U. calvus* its length is only about 65 per cent that of the cephalon. In *Estoniops* the corresponding figure ranges from some 78–79 per cent (*E. exilis*; Schmidt 1881, pl. 1, fig. 20) to about 85 per cent (*E. panderi*). The difference in width is still more pronounced: in *E. panderi* the pygidial width is about 75–76 per cent of the cephalic width, in *U. calvus* only 52–53 per cent. Moreover, the pygidium of *Upplandiops* has only a few, weakly marked pleural furrows.

Occurrence. As for the type species.

Upplandiops calvus sp. nov.

Plate 3, figs 1, 3–4, 6

v.1960 *Estoniops* n. sp.; Jaanusson, pp. 234, 279.
v.1963 *Estoniops* n. sp.; Jaanusson, pp. 21, 29, 37.
v.1966 *Estoniops* n. sp.; Männil, fig. 12 (range Clc).
v.1976 *Estoniops* n. sp.; Jaanusson, text-fig. 9 (range).

Derivation of name. Latin *calvus*, bald, alluding to the impression of the glabella seen in anterior view.

Holotype. Complete but partly disarticulated specimen (Pl. 3, fig. 1*a–c*), RM Ar55040, from an erratic boulder at Estuna, the province of Uppland. Furudal Limestone (*Hustedograptus teretiusculus* Zone).

Other material. Two exoskeletons (RM Ar55042, Ar50494), about 10 cephala and 10 pygidia (see 'occurrence' below).

Diagnosis. The genus is monotypic; see generic diagnosis.

Description. Cephalon fairly short (sag.), wide; length equals 40–42 per cent of width. Anterior cephalic margin broadly rounded, boundary between dorsal surface and doublure poorly defined, not reflected even in sculpture. In strictly dorsal view (Pl. 3, figs 1*a*, 4*c*) a slight change in width and convexity gives the impression of a lateral termination of the frontal glabellar lobe at about the level of the most lateral extent of the facial suture. No trace of a vincular furrow (Pl. 3, fig. 6*b*).

Dorsal furrow deep, overhung by adaxial edge of fixed cheek, between S2 and S3 running in an extremely narrow tunnel below a bridge formed by L3 and anterior of palpebral lobe. Fossula situated directly anterior to

first lens file of eye. L3 relatively short (exsag.); shape varying from almost parallel-sided (Pl. 3, fig. 4*c*) to somewhat triangular (Pl. 3, fig. 1*a*). L1 and L2 of about equal length (exsag.), with axes strictly transversely directed. Occipital ring about as wide as glabella across L3.

Eyes 47–48 per cent of length (sag.) of cephalon. Visual surface of 15 files of up to 6 lenses; eye formula in largest available cephalon (Pl. 3, fig. 4) 345 656 666 555 543, from front backwards. Central portion of glabella with low, composite tubercles of varying size, between and on which is a very fine granulation which extends to the borders, doublure and central cheek portions. In specimens with best preserved surface very shallow pits can be discerned on the genal field. Hypostoma unknown.

All three specimens with thorax preserved have ten thoracic segments.

Length of pygidium (excluding the articulating half-ring) equal to 64–66 per cent and its width to 52–53 per cent of the respective dimensions of the cephalon. It is comparatively broad, 2·5–2·6 times wider than long, weakly convex. Pygidial rachis weakly convex, relatively wide, maximum width at first rachial ring equal to 38–39 per cent of total pygidial width. Three rachial rings, defined laterally by deep furrows but medially almost obsolete, in best preserved specimens marked by very faint furrows. Posterior portion short, occasionally with one or two faint, transverse depressions medially. Pleural areas of pygidium weakly convex, with three pairs of poorly discernible pleural furrows and, in best-preserved pygidia, with an indication of an interpleural furrow on the anteriormost rib.

Occurrence. Uhaku Stage (*Hustedograptus teretiusculus* Zone) of Sweden and southern Estonia. Siljan district, Furudal Limestone, Fjäcka section. Northern Öland, Persnäs Limestone, Böda Hamn boring. Uppland, erratic boulders of the Furudal Limestone derived from the South Bothnian submarine Cambro-Ordovician sequence; among the records of *P. exilis* by Wiman (1908) specimens (housed in PMU) from the following boulders belong to *U. calvus*: Ekeby 5 and 57, Harg 2, Kristineholm 2, Salsta 3, Sunnersta 2, and Torrön 4 and 7. In addition, the species is common in the boulder Bergsbrunna 1 and occurs in a boulder from Estuna (RM). Southern Estonia, Uhaku Stage, Karula boring (430·4 m, 430·9 m).

Genus KEILAPYGE gen. nov.

Derivation of name. From Keila, a town in northwest Estonia, with a quarry in which F. Schmidt found much of the material of the type species. Gender feminine.

Type species. *Phacops* (*Pterygometopus*) *laevigatus* Schmidt, 1881.

Other species. *Estoniops latus* Antsygin, 1970, from the upper Middle Ordovician Cherdyn Stage, western slope of the central Ural mountains. A probable additional species, which differs by its relatively coarsely granulate glabella (Schmidt 1881, p. 235, fig. 13) occurs in the Keila Stage of northern Estonia (see also Schmidt 1907, p. 3). A poorly preserved specimen of *Keilapyge* was figured as *Estoniops* (*Pterygometopus*) sp. by Neben and Krueger (1979, pl. 143, figs 25–27) from erratics on the island of Sylt in northern Germany.

Diagnosis. Cephalic margin anteriorly broadly rounded (sag.), without admarginal furrow. Transsutural wing short (tr.). L3 long (exsag.). Eyes relatively small; anterior end of visual surface

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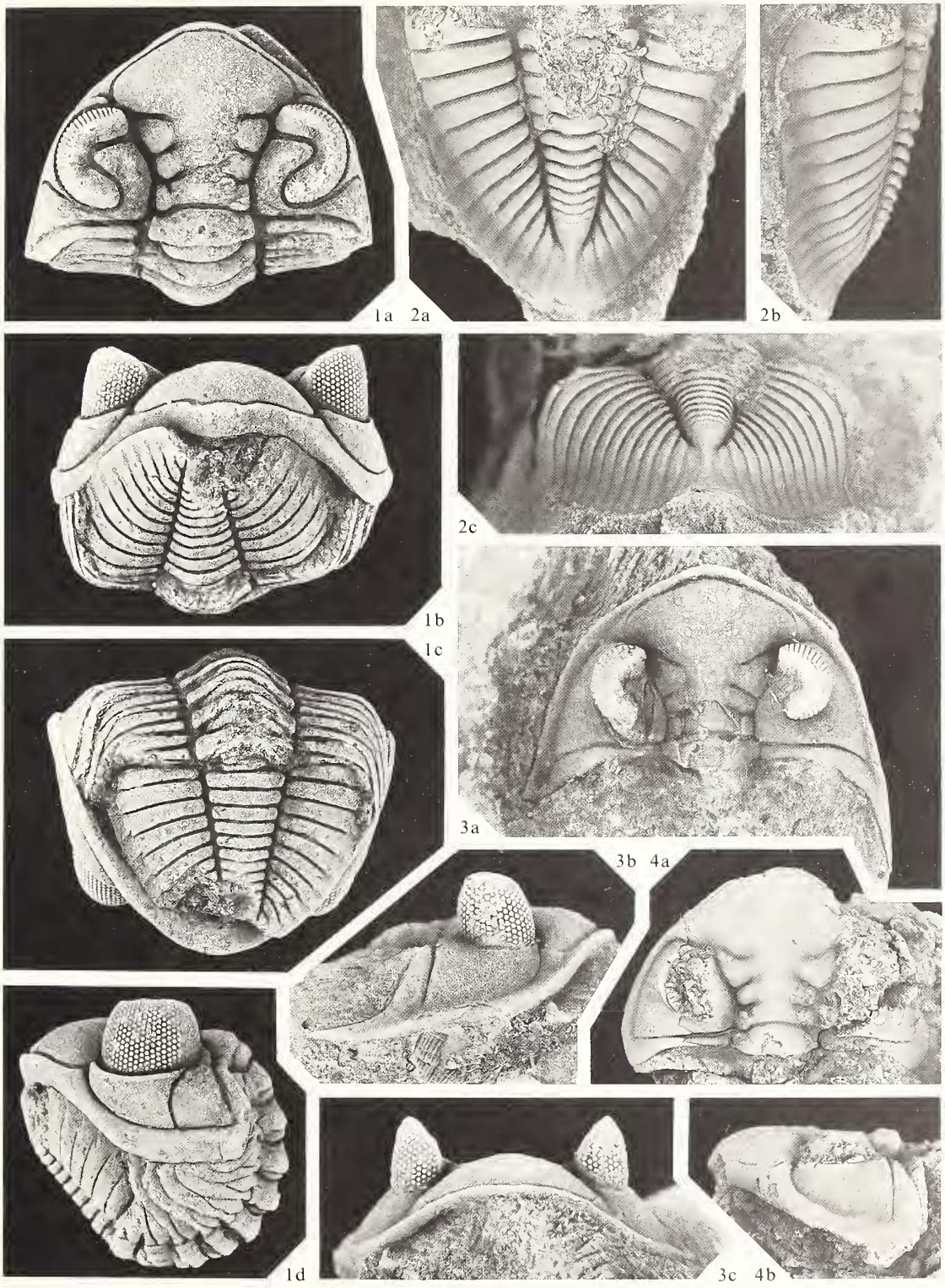
EXPLANATION OF PLATE 5

Fig. 1. *Ingriops trigonocephalus* (Schmidt, 1881); Voka Beds?, Kunda Stage (*Didymograptus artus* Zone); Pavlovsk, Ingria, western Russia. 1*a–d*, RM Ar38514, syntype; dorsal, anterior cephalic, dorsal pygidial, and lateral views of an enrolled exoskeleton, ×3.

Figs 2–3. *Achatella* (*Vironiaspis*) *kuckersianus* (Schmidt, 1881); Viivikonna Formation, Kiviõli Member, Kukruse Stage (*Nemagraptus gracilis* Zone); northeast Estonia. 2*a–c*, ETAGI Tr 3612; Kohtla; dorsal, lateral, and posterior views of pygidium (mainly internal mould), ×4. 3*a–c*, RM Ar50493; Kukruse; dorsal, lateral, and anterior views of cephalon, ×6.

Fig. 4. *Achatella* (*s.l.*) *schmidti* (Warburg, 1925); Boda Limestone, Ashgill; Osmundsberget, Dalarna, Sweden. 4*a–b*, PMU D189, holotype; dorsal and lateral views, exoskeleton preserved on cheek area only; figured by Warburg 1925, pl. 11, figs 27–28, ×4.



JAANUSSON and RAMSKÖLD, *Ingriops*, *Achatella*

reaches about mid-length of L3. Fixed cheeks provided, at level of L2, with a characteristic, medially pointed ridge. No vincular furrow. Genal angles rounded. Pygidium with semicircular outline; four or five pleural furrows.

Discussion. Keilapyge is distinguished from other comparable pterygometopines, such as *Estoniops* and *Upplandiops* gen. nov., by a set of distinctive cephalic characters. The eyes are comparatively small and reach anteriorly only to about the level of mid-length (exsag.) of L3. In the type species the length (exsag.) of the eyes is 32–34 per cent of cephalic length (sag.), and the visual surface is composed of 15 files of up to 6 lenses (counts in material from the Ristna beds). *K. lata* (Antsygin 1970, pl. 5, fig. 7) appears to have a comparable relative length of the eyes. Transsutural wings of the frontal lobe are distinct but short (tr.). The course of the anterior branch of the facial suture is best visible on Pl. 4, fig. 3*a* (left side) where exfoliation of the exoskeleton follows the suture (it is not visible on Pl. 4, fig. 1). L3 is proportionally very long (exsag.) and with a slightly posteriorly protruding posterolateral corner. A feature which is unique for *Keilapyge* is the development of a medially pointed ridge on the fixed cheek at the level of L1, constricting the dorsal furrow. The ridge is distinct in both *K. laevigata* (Pl. 4, fig. 1*a*, *d*) and *K. lata* (Antsygin 1970, pl. 5, figs 6–7), and also in *K.* sp. indet. (Neben and Krueger 1979, pl. 143, fig. 25).

The pygidium appears to have approximately the same size relative to the cephalon as in *E. exilis*. The type species has four pairs of distinct pleural furrows and a trace of a fifth pair (Pl. 4, fig. 5; Schmidt 1881, pl. 15, fig. 26). The pleural ribs are flat, with very faint traces of interpleural furrows. The pygidia which Antsygin (1970, pl. 5, figs 8–9) attributed to *K. lata* have five pairs of pleural furrows which extend almost to the pygidial margin and distinct interpleural furrows. They are very similar to the pygidia which Antsygin (1970, pl. 4, figs 14–16) referred to *Estoniops exilis*, and it is difficult to say how certain the attribution is of these pygidia to *K. lata*.

Occurrence. Jõhvi and Keila Stages (uppermost *Diplograptus multidens* to lowermost *Dicranograptus clingani* Zones) of northern Estonia and upper Middle Ordovician of the western slope of the central Ural mountains.

Genus ACHATELLA Delo, 1935

Type species. Dalmanites achates Billings, 1860, by original designation (for distribution see Ludvigsen and Chatterton 1982).

Diagnosis. Cephalon fairly flat. L3 triangular, with pointed anterolateral termination; S3 long, anterolaterally directed, straight or faintly posteriorly curved; distance (exsag.) between adaxial terminations of S2 and S3 less than half the length of L3 along dorsal furrow. Anterior branch of facial suture runs just outside the preglabellar furrow where developed. Transsutural wings or equivalent structures short (tr.). No vincular furrow. Pygidium with subparabolic outline, 10 to 14 pleural furrows.

Discussion. Achatella as currently defined appears to constitute a well-defined monophyletic group of species, but it displays a morphological variation that is quite extraordinary for a dalmanitacean genus. Genal spines can be long (Ludvigsen and Chatterton 1982, fig. 3) to absent (Pl. 5, fig. 4). The eyes can be comparatively short (exsag.), anteriorly not reaching the dorsal furrow (Ludvigsen and Chatterton 1982, pl. 1, fig. 7), or fairly long and reaching the dorsal furrow as far forwards as in front of L3 (Pl. 5, fig. 3). A subocular furrow can be distinct (Ludvigsen and Chatterton 1982, pl. 1, fig. 7) or absent (Pl. 5, fig. 3), and the absence of the furrow is unique for the whole subfamily. The development of the preglabellar furrow can be comparable to that of *Pterygometopus* (Pl. 5, fig. 3) or the furrow can be effaced laterally; in the latter case the frontal glabellar lobe is prolonged laterally into short transsutural wings. The development of the preglabellar furrow varies even medially because in some Ashgillian species from Scotland the furrow appears to be obsolete or nearly so. A group of species which, also with respect to other characters, are close to the type

species of *Achatella* have long (tr.) lateral glabellar furrows with S2 conspicuously shallowing close to the dorsal furrow, whereas in some other species (Pl. 5, fig. 3*a*) these furrows are relatively short and S2 does not shallow laterally. Outer portion of the pygidial pleural area varies from convex (Tripp and Morris 1986, pl. 4, fig. 2) to fairly strongly concave (Pl. 5, fig. 2). On the pygidium the interpleural furrows can be fairly distinctly marked (Ludvigsen and Chatterton 1982, pl. 1, fig. 1) to obsolete (Pl. 5, fig. 2).

It is clear that *Achatella* as currently defined requires revision but, as the distribution of the genus is mainly outside the Baltoscandian basin, such a revision is beyond the scope of this paper. An early representative of the genus from Baltoscandia differs from the other forms to such an extent that it is here included in a new subgenus, *A.* (*Vironiaspis*).

A species with a doubtful position within *Achatella* is *Pterygometopus schmidti* Warburg, 1925, known only from a single fragmentary cephalon (Pl. 5, fig. 4; Warburg 1925, pl. 11, figs 27–28) from the post-*Pleurograptus linearis* Zone Ashgill Boda Limestone of the Siljan district in Sweden. The general relative flatness of the cephalon and the pronouncedly triangular shape of L3 of this species is *Achatella*-like. The frontal lobe is defined, both anteriorly and laterally, by a preglabellar furrow which follows the facial suture as in *A.* (*Vironiaspis*) *kuckersiana*, but the furrow is narrower and shallower and becomes obsolete posteriorly a short distance before reaching the dorsal furrow. The anterior branch of the facial suture runs just outside the preglabellar furrow. A subocular furrow is distinct. In contrast to other species of *Achatella*, *A.* (*s. l.*) *schmidti* lacks genal spines. Without further information on the morphology the relationships of the species remain unclear.

Subgenus ACHATELLA (ACHATELLA) Delo, 1935

Type species. As for genus.

Other species. For North American species see Ludvigsen and Chatterton (1982). European species: *Phacops* (*Chasmops*) *bailyi* Salter, 1864 from the early Caradocian Tramore Limestone of Ireland; *Phacops* (*Pterygometopus*) *nieszkowskii* Schmidt, 1881, from the Rakvere Stage of northern Estonia; *Achatella consobrina* Tripp, 1954, from the Kiln Mudstones at Craighead Quarry near Girvan, south-western Scotland.

A new species of *Achatella* (*Achatella*), similar to *A.* (*A.*) *nieszkowskii*, is represented by a cephalon (Paleontologisk Museum, Oslo no. 131629) from the Mjösa Limestone at Bergsvika on Helgöya in the Mjösa district of the Oslo Region, Norway. A fragmentary cephalon (Paleontologisk Museum, Oslo no. 21991) from the Furuberget Formation (*Cyclocrinus* beds) at Furuberget in the same district may be conspecific. The latter specimen was recorded by Holtedahl (1910, p. 36) and Størmer (1953, p. 104) as *Pterygometopus kuckersianus*.

In addition, there is a group of late Ordovician species, included in *Achatella* by Morris (1988), which, pending additional information on their cephalic and pygidial morphology, are only tentatively included in the nominal subgenus. Such species are *Phacops truncatocaudatus* Portlock, 1843, from the Killey Bridge Formation of the Pomeroy district in Northern Ireland, *Phacops* (*Pterygometopus*) *retardatus* Reed, 1914, from the South Threave Formation, Starfish Bed, in the Girvan district, southwest Scotland (Morris and Tripp 1986, pl. 4, fig. 2), and *Phacops* (*Pterygometopus*) *quarrelensis* Reed, 1930, from the Quarrel Hill Formation, Lower Drummuck Group in the Girvan district. Specimens, identified as *Achatella* cf. *truncatocaudata*, have been recorded from the Hirnantian High Mains Formation of the Girvan district (Owen 1986, fig. 2*a–e*).

Diagnosis. Glabellar furrows tend to be comparatively long, with S2 very shallow close to the dorsal furrow but deepening medially. Eyes of moderate size, with the anterior end some distance from the dorsal furrow. Subocular furrow distinct. Outer portion of the pygidial pleural area convex to weakly concave.

Discussion. The type species was described in detail by Ludvigsen and Chatterton (1982, p. 2184, pl. 1, figs 1–7).

Examination of cephala of *A.* (*A.*) *nieszkowskii* from Estonia revealed that the species is markedly similar to *A.* (*A.*) *achates* in many important respects, such as the size and position of the eyes,

shallowing S2 laterally, relative length of glabellar furrows, and development of the subocular furrow, and that it differs in these respects from the Estonian Middle Ordovician species which Männil (1958) included in *Achatella*.

Occurrence. North American Midcontinent region, Shermanian to Edenian Stages (approximately lower *Dicranograptus clingani* to topmost *Pleurograptus linearis* Zones). Western Ireland, Tramore Limestone (upper *Nemagraptus gracilis* Zone?). Scotland, Girvan district, Kiln Mudstone (*Dicranograptus clingani* Zone). Norway, Oslo Region, Furuberget and Mjösa Formations (*Dicranograptus clingani* Zone). Estonia, Rakvere Stage (uppermost *Dicranograptus clingani* Zone). For distribution of the species which are questionably included, see above.

Subgenus ACHATELLA (VIRONIASPIS) subgen. nov.

Derivation of name. From the name of the north-eastern Estonian province of Viru, latinized Vironia, the district where the type species is found. Gender feminine.

Type species. *Phacops* (*Pterygometopus*) *kuckersianus* Schmidt, 1881 from the Kukruse Stage of northern Estonia.

Other species. Tentatively assigned: *Phacops* (*Pterygometopus*) *kegelensis* Schmidt, 1881, from the Keila Stage of northern Estonia.

Diagnosis. Glabellar furrows of moderate length, with S2 not at all, or only slightly shallowing towards the dorsal furrow. Eyes fairly large, their anterior end reaching the dorsal furrow. Subocular furrow not developed. Outer portion of pygidial pleural area distinctly concave.

Discussion. *A*. (*Vironiaspis*) differs from the nominal subgenus by the following main features:

(1) The eyes reach the dorsal furrow, slightly in front of L3 in the type species.

(2) The lack of both a subocular furrow and a distinct subocular ridge; there is only a faint, narrow, groove-like constriction of the base of the eye as in many other dalmanitaceans.

(3) The lateral glabellar furrows are comparatively short (tr.) and S2 lacks the distinct abaxial shallowing developed in all species unconditionally included in the nominal subgenus in this paper.

(4) The outer portion of the pygidial pleural area is conspicuously more concave than in any other species referred to *Achatella*.

In *A*. (*Vironiaspis*) *kuckersiana* the frontal glabellar lobe is defined, both anteriorly and laterally, by a narrow but distinct preglabellar furrow (Pl. 5, fig. 3*a*), comparable to that in *Pterygometopus*, and as in the latter genus the facial suture (not visible on our photograph) runs just outside the furrow. An equivalent to the transsutural wing of the frontal lobe is situated lateral to the preglabellar furrow and thus outside the glabella. Its anterolateral boundary is defined by the cephalic border furrow which becomes effaced anteromedially in front of the preglabellar furrow. A detailed comparison with the development of comparable structures in some species of *A*. (*Achatella*) (e.g. Tripp 1954, pl. 4, figs 26*a–c*, 27; Ludvigsen and Chatterton 1982, pl. 1, fig. 7) is difficult without examining the specimens.

A. (*Vironiaspis*?) *kegelensis*, tentatively included in the subgenus, is a rare species and the material available in Estonian museums is fragmentary. It is not quite certain that the cephala referred to this species from the erratic boulders of northern Germany (Neben and Krueger 1979, pl. 125, figs 16–17; pl. 142, figs 6–7) are conspecific.

Occurrence. Uhaku (Rõõmusoks 1970, p. 9; *Hustedograptus teretiusculus* Zone), Kukruse (*Nemagraptus gracilis* Zone), Jõhvi (upper *Diplograptus multidens* Zone), and Keila (lower *Dicranograptus clingani* Zone) Stages of northern Estonia.

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